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Fog drip maintains dry season ecological function in a California coastal pine forest

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Abstract. Fog drip is recognized as an important source of water for many ecosystems that often harbor a disproportionate fraction of endemic species. Characterizing and quantifying the ecological importance of fog drip in these ecosystems requires a range of approaches. We report on a multi-faceted study of Bishop pine (*Pinus muricata* D. Don) along a coastal-inland transect on an island off Southern California. Hourly sampling included micrometeorology, sap flux, and soil moisture. Monthly measurements included changes in tree girth, plant water stress, and isotopic values of fogwater, rainwater, and xylem water. These data show that summertime fog drip clearly affected soil moisture and maintained aspects of tree function, including leaf water relations, sap flux dynamics, and growth rates. Although water from fog drip to the soil surface was occasionally taken up by pine trees, as quantified with isotopic measurements and a Bayesian mixing model, this utilization of fog drip was highly variable in space and time. The proportion of fogwater inferred to have been used is also much less than has been demonstrated in more mesic coastal forest ecosystems using isotopic methods. These results thus suggest high ecosystem sensitivity to even moderate amounts of fog drip, a finding with important implications as climate change differentially affects fog and rain patterns.

Key words: Bayesian modeling; Bishop pine; cloud forest; cloud shading; drought; ecohydrology; fog drip; Mediterranean ecosystems; *Pinus muricata*; water stable isotopes.

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Introduction

Assessing and quantifying the ecological importance of fogwater to forest function has challenged researchers for more than a century (e.g., Marloth 1905, Scholl et al. 2011). Fog drip has been shown to be an important source of water in a number of ecosystems, including tropical and temperate montane cloud forests and coastal ecosystems in the world's five major Mediterranean climate zones. These ecosystems are recognized for high levels of biodiversity and species endemism (Olson and Dinerstein 1998). In tropical cloud forests, a large percentage of the total ecosystem water inputs may come from regular, even daily, fog inundation throughout the year (Bruijnzeel and Veneklaas 1998, Hamilton et al. 2012). In Mediterranean climate regions like coastal California, however, water inputs are highly seasonal, with most rain falling in winter, followed by a long summer drought as stored soil moisture steadily

declines. Year-round water availability is critical to both individual and population-level survival of many of the drought-sensitive evergreen species found in this region (Baguskas et al. 2014). The only significant summertime ecosystem water input is fog drip, and it can play a key role in maintaining some level of water availability through the summer (Carbone et al. 2012).

For these reasons, the influence of fog (surface-level clouds) on ecological and hydrological processes has long intrigued scientists studying such coastal ecosystems. This attention is understandable, given the high frequency of summer fog when rainfall is rare and temperature and solar irradiance are highest. On this basis alone, a number of researchers have inferred an important role for fog in the ecological functioning of coastal ecosystems, since it influences fundamental environmental conditions like humidity, temperature, and irradiance. However, despite this history, there is little process-level research to support how or why plants, many of them endemic to fog-belt areas, should prefer foggy regions and how fog alters the environment; importantly, there is insufficient work quantifying water delivered by fog drip and its ecological consequences except for a few notable sites. Because climate change may alter coastal fog dynamics, assessing and quantifying its ecological importance—especially the sensitivity of vegetation to even small amounts of fog drip—is critical. Thus, a better assessment of ecosystem sensitivity to fog drip is required for any projections of ecological responses to climate change in this region.

Studies using isotopic methods to quantify the ecological importance of fogwater to vegetation in cloud forests and along Mediterranean-climate coastlines have in some cases found large percentages of total annual transpiration coming from fogwater (Dawson 1998, Corbin et al. 2005, Scholl et al. 2011). This approach relies on the isotopic distinction that generally exists between fogwater and rainwater (Gonfiantini and Longinelli 1962, Ingraham and Matthews 1995, Gat 1996, Dawson 1998, Scholl et al. 2011). The degree of isotopic separation between fogwater and rainwater varies regionally, with coastal California having some of the largest separations, principally due to the temporal separation of the winter rain and summer fog seasons (Scholl et al. 2011). This separation can enable the use of natural abundance stable isotopes as tracers of rain and fogwater through the soil and into plant tissues to quantify the relative contributions of these water sources to individual plants (Ingraham and Matthews 1995, Dawson 1998, Feild and Dawson 1998).

Previous research using non-isotopic approaches has suggested that Bishop pines (*Pinus muricata* D. Don) on Santa Cruz Island and Torrey pines (*Pinus torreyana* ssp. *insularis* J. R. Haller) on adjacent Santa Rosa Island benefit from fogwater on a variety of time scales. Williams et al. (2008) showed that Torrey pine growth was significantly positively correlated with summer fog inundation. Bishop pine stand dynamics on Santa Cruz Island (SCI) over the last century have included episodic pine expansion from core areas and massive die-backs following droughts. Hydrologic modeling to explain these spatio-temporal mortality dynamics was successful only when incorporating fogwater inputs (Fischer et al. 2009). Similarly, Baguskas et al. (2014) demonstrated that the spatial distribution of cloud frequency was one of the primary predictors of the spatial distribution of pine mortality following a drought in the middle of the last decade. Baguskas et al. (2016) showed that Bishop pine sapling trees are more vulnerable to experiencing water stress during summertime compared to adult trees; however, sapling trees also benefit more from fog drip than do adult trees, a finding that has implications for population dynamics of this stand during future droughts. Finally, Carbone et al. (2012) showed that fogwater was important for a range of ecosystem processes at sites with contrasting fog inputs, ranging from plant water movement to soil respiration to microbial activity to patterns of summertime tree growth.

We adopted a multifaceted approach to better understand how summer fog influences several aspects of plant function, with a particular focus on plant water relations. A related objective was to further characterize the ecological importance of fogwater to a rare and drought-sensitive ecosystem (Southern California Bishop pine woodland), as well as to quantify spatial variability in rain and fog inputs across a coast-to-inland transect. Our approach included extensive weather

and ecological data collection, as well as monthly sampling of fog, rain, soil, and plant water for isotopic composition measurements used to quantify spatial and temporal fogwater uptake by Bishop pine trees.

Materials and Methods

Weather and soil moisture measurements

Our study area was on Santa Cruz Island, 40 km south of Santa Barbara, California. Our sites were located along a coast-inland transect that spanned the southernmost stand of Bishop pines (*Pinus muricata* D. Don) in the United States. Weather stations were installed along what we refer to as the SCI transect (Fig. 1, Fischer et al. 2009). These sites span a large gradient in cloud cover, fog drip and rainfall, and potential evapotranspiration: sites nearest the coast experience the highest cloud cover and lowest summertime evapotranspiration, while the reverse is true of the most inland sites. Sites 1 and 10 had existing weather stations maintained by California State University, Northridge (J. B. Wall, *personal communication* 2006). We installed additional sensors at these sites in April 2004: fog collectors, leaf wetness sensors, and soil moisture sensors. At the same time Sites 2, 8, 11, and 12 were instrumented with Hobo weather stations (Onset Computer Corp., Bourne, Massachusetts, USA) with the above-listed sensors plus rainfall, temperature, relative humidity, wind speed and direction, and photosynthetically active radiation.

Sites 7 and 9 were instrumented with Campbell Scientific (Logan, Utah, USA) weather stations, along with more extensive measurements of soil moisture and temperature. Site 7 had all the above-listed weather sensors, including leaf wetness measurements in the canopy and at the soil surface; additionally, three soil profiles were instrumented to record soil moisture and temperature at different depths. Water potential sensors (gypsum blocks, Campbell Scientific #227) measured water potential both inside and outside the tree canopy at Site 7 from 2 to 15 cm depth. Volumetric water content sensors (time domain reflectrometry (TDR) probes, Campbell Scientific CS616) measured soil water in the upper 10 cm in both profiles (inside and outside of the tree canopy). Soil temperatures were recorded at 25 and 50 cm under the canopy. A third profile was installed under the tree canopy to measure soil matric water potential and temperature at sixth depths (0–50 cm) using heat dissipation probes (Campbell Scientific #229). Soil water potential for these sensors was calculated following the methods of Flint et al. (2002).

As reported previously by Fischer and Still (2007), Fischer et al. (2009), and Carbone et al. (2012), the long-term mean winter rainfall measured at the ranch in the center of the island (Fig. 1) is 447 mm. Regression of monthly rainfall for 1998–2005 showed that Site 9 received 0.4% more rainfall than the long-term mean rainfall at the ranch site (r^2 = 0.92). Regression of daily rainfall for 2004–2005 showed that Site 7 received 61% as much rainfall as Site 9 (r^2 = 0.94; Fischer

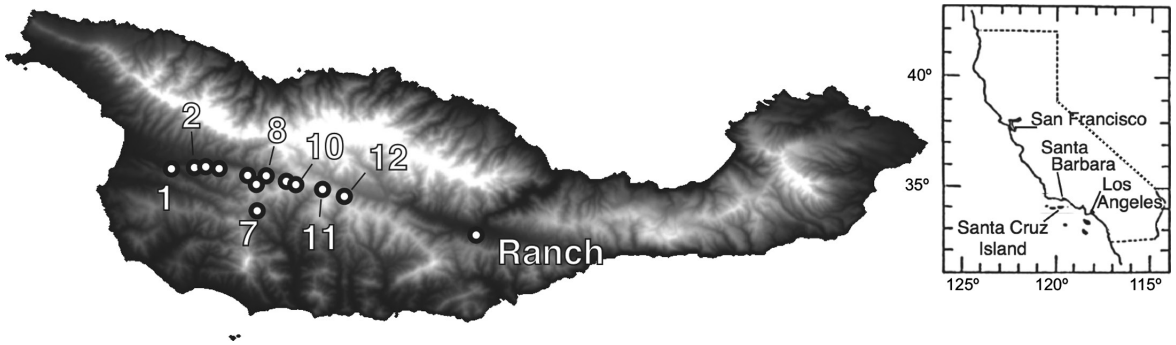

Fig. 1. Elevation map of Santa Cruz Island showing sites deployed on an W–E transect throughout the island's main stand of Bishop pines (*Pinus muricata* D. Don). Stations are numbered 1–12, from the coast inland. The island lies about 30 km off the Southern California coast, is 38 km long, and reaches 753 m elevation (figure from Fischer and Still 2007).

et al. 2009). Interannual rainfall in the study years was large: in winter 2004–2005, 755 mm of rain at Site 7 fell compared to 431 mm in winter 2005–2006.

Xylem pressure potential measurements

Xylem pressure potential was measured using small twigs placed in a pressure chamber (PMS Instrument Co., Albany, Oregon, USA). Repeat twigs from the same branch were measured until we were confident of the reading within ±0.025 MPa (usually three samples). Between 2005 and 2006, we measured monthly pressure potential of twigs from two to four branches at a consistent height on the tree (approximately 1 m from the ground) on each of two trees at Site 7 at predawn (in the hour before sunrise) and again midday (~11:00-noon). Predawn xylem pressure potential is generally considered indicative of the maximum soil water potential in the rhizosphere (Dawson 1993). Midday xylem pressure potential represents maximum daily drought stress, with −1.5 MPa being the permanent wilting point for many crop plants (Lambers et al. 1998). All midday measurements were made on twigs that had been sealed in aluminized bags for at least 1 h.

Sap flux measurements

Site 9 was installed in September 2005 with the same weather sensors as Site 7, plus an array of 10 thermal dissipation sap flux sensors (Dynamax Corp, Houston, Texas, USA) installed in seven adjacent Bishop pine trees. All trunks were wrapped with aluminized bubble wrap (Reflectix Corp., Markleville, Indiana, USA) in a 50 cm wide band at the sensor height (1–1.5 m, depending on branch spacing and trunk access) to reduce ambient temperature gradients resulting from solar heating of the probes, as these gradients can affect Granier-type heat dissipation probes that rely on temperature differences between adjacent heated and unheated probes to infer rates of sap flux (Granier 1985). We also removed a great deal of noise from the data by correcting all trees' sap flux records using the ambient gradients recorded by an unheated pair of probes in one tree (following methods of Lu et al. 2004). Another methodological issue with Granier-type probes is calibrating them to an assumed period of zero transpiration at night (Lu et al. 2004). Our zero values displayed significant fluctuations from night to night that might have been be related to nighttime transpiration (Burgess and Dawson 2004). Thus, we used each probe's lowest nighttime value in a 1-week moving window as zero transpiration. Sap flux velocity (10^{-6} $m^3 \cdot m^{-2} \cdot s^{-1}$) was then calculated using the formulas in Lu et al. (2004).

To better understand the mechanistic underpinnings of sap flux, we calculated reference evapotranspiration (ETref). ETref is a measure of the evaporative demand on vegetation that was developed for use in irrigation scheduling, and should be closely related to sap flux in trees. Extensive testing has validated the most recent formulation as accurately representing rates of evaporative water loss across a diversity of vegetation and climate types (Allen et al. 2005). We were also interested in a statistical model of sap flux, to infer its most important environmental drivers. We used the random forest algorithmic approach (package RANDOMFOREST in R, version 4.6-12) to create a predictive model of mean daytime summertime sap flux, and tested a range of possible drivers. Classification and regression tree approaches like random forest have some distinct advantages over conventional statistical regressions for our purposes: they do not require normally distributed data, they can capture complex and non-linear interactions between environmental predictor variables, and they can distinguish threshold values and responses of predictor variables (Olden et al. 2008). The predictor variables we tested included the following (mean daytime values): downwelling total shortwave radiation (W/m^2), photosynthetically active radiation (PAR in $\mu mol \cdot m^{-2} \cdot s^{-1}$), atmospheric vapor pressure deficit (VPD in kPa), relative humidity (%), air temperature (°C), and xylem pressure potential (MPa). We also included rainfall (mm/d), fog drip (mm/d), and running summertime sums of fog and rain inputs (mm). Of these possible predictor variables, we used only the three most important ones as selected by the random forest algorithm. We defined summertime as the period between 15 April 2006 and the end of our sap flux record on 22 August 2006. During this period, there was one storm with a total rainfall of ~25 mm (21–22 May), but multiple fog events.

Dendrometer measurements

Dendrometer bands were installed progressively across the stand of Bishop pines from June 2004 through June 2006, with most bands being located at sites 7 and 9. We used standard manual band dendrometers (Agricultural Electronics Corporation, Tucson, Arizona, USA), installed 0.5–1.5 m above ground (depending on branch patterns and trunk access). We attempted to sample a representative distribution of tree size classes at each site, and the circumference range varied from approximately 0.3 to 1.3 m. Bands were read on monthly sampling trips through Fall 2006, with readings made as close as possible to midday to minimize possible impacts of diurnal shrinking and swelling of trees (typically 0.1–0.2 mm) on our readings. The annual daily average temperature range at our sites is relatively small (10–15°C), and thus we did not correct our readings for the linear coefficient of thermal expansion specified for these bands (11.2 $\mu m \cdot m^{-1} \cdot °C^{-1}$). Actual dates of measurements varied somewhat from month to month, resulting in readings spaced 3–5 weeks apart. We interpolated daily growth rates (in mm circumference change per tree) between readings, and then averaged daily values for each calendar month (data from Williams 2006).

Fog and rain collection methods for isotopic measurements

In order to characterize the isotopic composition of water fluxes and pools, and to trace the relative importance of fogwater and rainwater to ecological processes in this ecosystem, we collected hundreds of water samples during monthly trips to our field sites on Santa Cruz Island from December 2003 to December 2006. During each trip, we collected samples of fog and rainwater that had accumulated since the last trip from up to 12 sites spread across the western pine stand (Fischer and Still 2007, Fig. 1). To collect fog samples, one or more harp-style fog collectors (Fischer and Still 2007) was installed at each site. Each collector was set up either to collect samples for isotopic analysis or to meter fogwater inputs for timing and quantity. Metering of fogwater inputs was done by plumbing the fog collector into a covered tipping bucket rain gage. The tipping buckets registered every 3.7 or 4.8 mL of water, depending on the site. Average collection volumes on foggy nights ranged from 22 to 186 mL across the sites (Fischer and Still 2007). Collection for isotopic analysis was done by plumbing the fog collector into a pair of 2 L amber HDPE collection bottles (Nalgene Corp., Rochester, New York, USA) using 6.5 mm (I.D.) UV-resistant Tygon tubing (Saint-Gobain Corp., Courbevoie, France). The bottles were connected so that overflow from the first bottle went to the second, and overflow from the second went out a vent tube. Rainwater was collected for isotopic analysis with a simple funnel plumbed into a 2 L bottle.

The collection bottles were fitted with long narrow tubes for both the inlet and a vent tube. In theory, a 6.5 mm interior diameter tube of 20 cm or more prevents most evaporation, because the diffusion path for water molecules becomes improbably long (Scholl et al. 2011). We used vent tubes 40–50 cm in length, longer than those that had been shown to prevent evaporation in other forest studies (T. E. Dawson, *personal communication*). Unfortunately, we discovered that diffusion was not the only potential evaporative pathway for water vapor leaving our bottles. Samples from a test bottle at the sunniest, easternmost site (Site 12) partially filled with water of known isotopic composition showed progressive enrichment each month over the summer of 2005, although there was no evidence of a differential isotopic fractionation between δ^2H and $\delta^{18}O$ (where

$$\delta = 1000 \times \left(\frac{R_{sam}}{R_{std}} - 1 \right)$$

and R_{sam} and R_{std} are the ratios of $^{18}O/^{16}O$ or $^2H/H$ in a sample or standard, respectively; $\delta^{18}O$ and δ^2H values are reported relative to the V-SMOW measurement scale). Such a differential kinetic isotope fractionation would be expected with diffusion of water vapor out the vent tube (Cappa et al. 2003, Luz et al. 2009). We infer that daily heating and cooling of air in the test bottle, which was sitting on bare soil, forced saturated air out of the bottle at midday, and drew drier air back in at night. This process of evaporative loss by mass flow without diffusion would explain the lack of differential fractionation. This enrichment effect would be expected to be strongest with the smallest water samples (largest volumes

of air exchange), during the warmest months, and at those stations with the least shading of the bottles (Sites 11 and 12). Most of our monthly samples had large volumes of water (>1000 mL) that would be much less susceptible to this enrichment.

To avoid further problems with evaporative enrichment in our fog, rain, and throughfall samples, beginning in January 2006 we floated a layer of mineral oil ~1 cm thick in each bottle to prevent evaporation into the headspace of the bottle (Scholl et al. 2011) and wrapped the bottles in aluminized bubblewrap (Reflectix, Inc.) to reduce air exchange from the bottle in any given daily thermal cycle. Subsequent to these changes even our test bottle (in full sun at Site 12 with small water volumes) showed no change in isotopic composition from May to October 2006. Algal growth in fog and rainwater collection bottles was resolved by adding copper sulfate to the collection bottles (~0.5 g per 2 L bottle) each month (T. E. Dawson, *personal communication*). Various insects created clogged collection tubing. Clogs were largely resolved by screening the inlet and vent tubes in summer 2004 for rain bottles, and in summer 2005 for fog bottles.

Each monthly rain and fogwater sample is a composite of all precipitation events from the previous month. However, when collection bottles overflowed in a given month, the last precipitation event may have been under- or over-represented in the bulk sample remaining in the bottle. The importance of such sampling bias is higher with rainfall than fog because the isotopic values of successive rain storms can differ widely in this area, as was reported by Fischer and Still (2007). Even minor sampling bias with such isotopically different sources can substantially skew volume-weighted seasonal rainfall averages. Fog events tend to vary much less, and thus this bias is not expected to be as consequential as it is with rain.

In addition to ecosystem water inputs (fog and rain), we measured the isotopic composition of water ultimately leaving the ecosystem as stream flow. Water samples were collected from late 2003 to early 2005 at the upper end of Cañada del Puerto, one of the only streams that flow aboveground throughout the year. The sampling point was just north of the main ranch (Fig. 1) where water from both east and west parts of the central valley merges and flows north over a bedrock sill to the sea. This stream continues to flow in the driest months of the driest years, draining deep layers of Quaternary alluvium that fill the central valley.

Soil and xylem water isotope collection methods

Surface soil samples (0–3 cm depth) were obtained with a trowel, after scraping away litter (typically 1–4 cm) and loose organic matter (typically no more than 1 cm). Deeper soil samples were obtained with a 2 cm diameter soil corer. Soil samples were partitioned in 3 cm depth increments and sealed in vials immediately after coring to minimize evaporative enrichment effects. Samples of pine xylem tissue and surface soil at each site were also collected for subsequent laboratory water extraction and isotopic analysis. To obtain xylem water samples, we clipped well-suberized twigs (twigs with mature bark) from a selected mature pine tree at each site. Twigs selected were generally 1–1.5 cm diameter at the base, with 6–8 yr of growth. After cutting off the growing tip of the twig, including all retained needles, we quickly stripped off the bark, clipped the twig into 3 cm lengths, and sealed those into vials.

All samples collected for stable isotope analysis in the field were placed into identical 20 mL glass scintillation vials with polycone lid inserts (Fisher Scientific, Waltham, Massachusetts, USA) to minimize evaporation. They were refrigerated for several days before being stored at −20°C until extraction (for soil and xylem water) and isotopic analysis using cryogenic vacuum distillation at the University of California, Santa Barbara (UCSB) following standard methods (Dawson 1993). The water samples from fog, rain, and vapor, as well as those extracted from xylem tissue and soil samples, were analyzed for isotopic composition at either the Center for Stable Isotope Biogeochemistry at UC Berkeley or the Marine Science Institute Analytical Lab at UCSB.

Bayesian isotope mixing model analyses

Recent advances allow the explicit propagation of error in Bayesian mixing model analyses (Moore and Semmens 2008, Parnell et al. 2010) that quantify the proportional contribution of source end-members to a measured sample. Statistical methods that incorporate variations in soil water isotope profiles

Table 1. Seasonal averages of fog and rainwater isotopic composition at Site 7 on Santa Cruz Island.

Precipitation type and year	$\delta^{18}O$	$\delta^{18}O$ SD	$\delta^{2}H$	$\delta^{2}H$ SD
Dry season fog				
2004	−1.8	0.5	−10.2	3.2
2005	−2.9	0.4	−11.4	2.3
2006	−3.0	0.4	−12.6	2.9
Wet season rain				
2004–2005	−5.8	3.7	−36.7	24.4
2005–2006	−4.5	2.6	−25.4	7.2
Stream water				
December 2003–January 2005	−4.4	0.4	−28.4	1.0

Notes: All values except 2004 summer fog are volume weighted. Also shown are the mean isotopic values of stream water, which serves to integrate the rainfall signal over multiple years.

and source end-members are increasingly being used to infer which soil depths contribute to plant water uptake (Ogle et al. 2004, Nippert and Knapp 2007, Prechsl et al. 2015). This provides information on plant rooting depth distributions and activity; variations in the relative sources of plant water (i.e., precipitation type) are of lesser interest in most cases. However, due to logistical difficulties and sample losses, we have very limited vertical soil water isotope data across depths at each site and across seasons. We did collect extensive fog, rain, and xylem isotope water data, which can be used to estimate the relative contributions of fog and rainwater sources to xylem water. This approach in effect assumes that precipitation inputs are not heavily modified by soil evaporation (both amounts and isotopic composition—discussed in *Results*), and that soil water isotope distributions convolved with plant active rooting depth distributions ultimately determine plant xylem water isotope composition.

In order to infer the proportional contributions of fog vs. rain to plant xylem water at a given site and for a given month, we used the SIAR Bayesian isotope mixing model (Parnell et al. 2010). We used the SIAR package in R (version 4.2) for all calculations. SIAR is a Bayesian statistical model and thus provides a way to incorporate isotopic variability in the sources (in this case, fog and rainwater) as well as in the materials analyzed (in this case, plant xylem water). The variability is propagated through the calculation and is thus explicitly represented in the posterior probability density distributions of source contributions (Parnell et al. 2010).

The model was run using the following measured isotopic values as input variables: xylem water values from each site and sampling period along with seasonal and interannual fog and rain sources, as well as their associated standard deviations (Table 1). For each model run using SIAR, parameters were kept constant at the following values: trophic enrichment factor = 0; number of model iterations = 500,000; number of initial model iterations to discard = 50,000; no concentration dependence, i.e., concdep = 0. Another advantage of the Bayesian framework is the incorporation of prior information in the calculation. In our case, the standard Dirichlet prior distribution treats each source as independent from one another and assumes that sources sum to unity (Parnell et al. 2010). This is reasonable in our case, as summer fog and winter rain are independent in quantity (Williams et al. 2008) and isotopic value (Fischer and Still 2007). They should also be the only water sources for plants at our sites, as there is no groundwater source (the sites are all located on steep ridgelines), and dewfall should provide minimal plant water as documented by leaf wetness sensors at the soil surface at Site 7 (data not shown).

Results

Soil moisture data

Soil moisture probes measuring water potential at Site 7 exhibit dynamic behaviors at different depths that are driven by soil drying following the last rains and regular light fog-drip to the soil surface (Fig. 2a). Surface soils (0–15 cm) both inside and outside the pine canopy dried substantially prior to the last rains (on 28 April and 9 May; Fig. 2a) of the unusually rainy 2005 wet season. After rewetting with rain, the soil outside the tree canopy at Site 7 (light gray lines, labeled 'O') became drier than the permanent wilting point (−1.5 MPa; also the effective measurement limit of these sensors) within 2 weeks. By contrast, soils under the tree canopy (black lines labeled 'In') received fog drip repeatedly throughout the summer (gray bars, right axis) and remained moist until late August, particularly in the

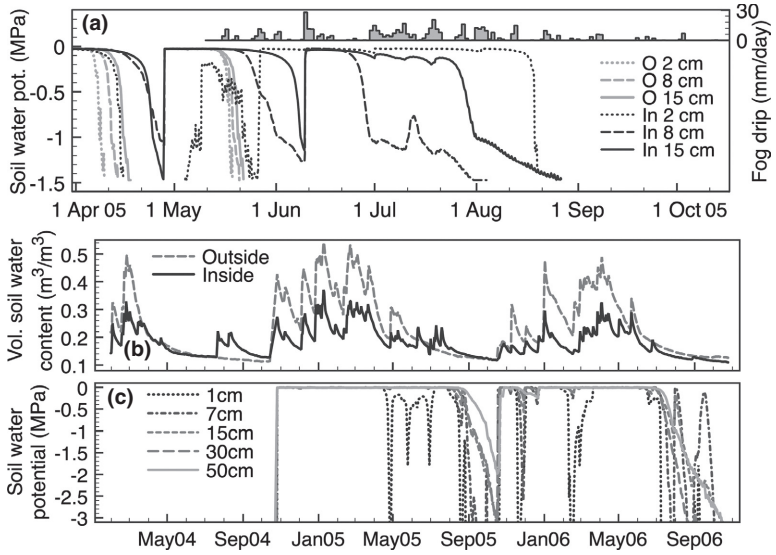

Fig. 2. (a) Summer 2005 soil water potential (left axis) and fog drip (right axis) at Site 7. Soil water potential (in MPa) was logged hourly in two profiles located 10 m apart, one just outside (O, gray lines) and the second inside (In, black lines) the tree canopy. Dotted lines represent sensors closest to the surface in both locations. Daily fog drip at Site 7 was estimated from fog collection volumes assessed with a fog collector placed outside the pine canopy and adjacent to the weather station. (b) Soil water content 2004–2006 at Site 7. Volumetric soil water content from two TDR probes installed inside and outside the pine canopy. (c) Soil water potential from 2005 to 2006 at multiple depths under tree A at Site 7 measured with heat dissipation probes.

shallowest soils (2 cm). Thus, the period between the last winter rainfall and the time when soils had dried below −1.5 MPa was extended from ~2 weeks without fog drip (outside the canopy) to ~15 weeks with fog drip (inside the canopy) (Fig. 2a). Of course, differences in the post-rain dry-down rate would be expected based on canopy cover affecting the amount of solar radiation reaching the soil surface (trees vs. grasses), as well as differences in the rate of soil water withdrawal from active pine trees compared to senesced grasses. Despite these other factors, fog drip beneath the pine canopy unambiguously enhances soil water availability during most of the rain-free summer.

A similar pattern over a longer time period at Site 7 is shown with probes measuring volumetric soil water content (0–10 cm) inside and outside the tree canopy (Fig. 2b). The summer of 2004, which followed a drier than average winter, experienced a particularly strong pulse of fogwater in July and August. Soil water potential data collected in the later portion of this time period (October 2004 through October 2006) using different sensors at several depths under the canopy show a general pattern of drying from the top down as expected, although there are notable exceptions in the summer when surface soils are re-wetted by fog drip (Fig. 2c). The sensor at 1 cm shows frequent large changes in water potential that correspond with fog drip events. Thus, our soil moisture sensors show unambiguous evidence of substantial fog drip to the soil surface in the otherwise dry and rain-free summertime months (May–Sep). As shown by Carbone et al. (2011), frequent re-wetting of the soil from fog drip throughout the summer at this site drives large and transient pulses of soil respiration associated with both heterotrophic and autotrophic sources.

Xylem pressure potential

Xylem pressure potential measurements of two Bishop pine trees at Site 7 showed a seasonal pattern of increasing water stress throughout the summer (Fig. 3a). However, the decline in predawn xylem pressure potential in the summer of 2005 and 2006 was not as severe as might be expected after several months without rain: predawn xylem pressure did not fall

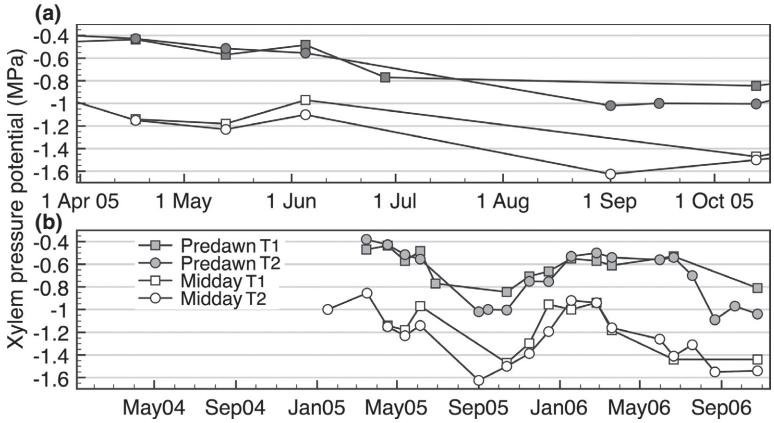

Fig. 3. (a) Twig xylem pressure potential measured on the same two trees at Site 7 during summer 2005. (b) Xylem pressure potentials from 2005 to 2006 for trees T1 and T2 at Site 7. Lines connecting points are for visual reference only.

below −1.2 MPa even in early fall (September) of 2006, which followed a drier than normal winter (Fig. 3b). Note that both the 8 and 15 cm soil water potential sensors in Fig. 2a show an abrupt decrease in rate of drying at −1 MPa in summer 2005. This corresponds with the driest predawn xylem pressure potentials recorded that summer, and suggests that trees had access to −1 MPa water deeper in the profile throughout the dry season. Midday xylem pressure measurements were all significantly more negative than predawn values, and reached a limit of about −1.45 MPa for tree 1 and −1.6 MPa for tree 2 in both summers, even though summer 2005 followed a very wet winter compared to summer 2006.

The difference between predawn and midday xylem pressure is generally greatest from July to September (Fig. 3b). This suggests that later in the summer the trees exhibit earlier daily stomatal closure to limit midday drought stress as the summertime drought intensifies. Other pine species, many of which are isohydric like closely related Monterey pine (*Pinus radiata* D. Don), are known to exert strong stomatal control to prevent midday xylem pressure values from becoming too negative, implying that Bishop pines are also isohydric (Waring and Silvester 1994, West et al. 2007, Meinzer et al. 2014). This strong stomatal control protects against xylem embolism, but at the expense of strongly limiting carbon assimilation and growth potentials. Higher temporal resolution sampling would undoubtedly have revealed much more day-to-day variability in xylem pressure potential, and this would likely be driven by day-to-day variations in fog drip and cloud shading. For instance, the predawn pressure measurements taken on 5 June and 28 June of 2005 occurred just before and then 2 weeks after a significant fog drip period during which surface soils were much wetter, i.e., these samplings bracketed the event without actually sampling it (Fig. 3a). Similarly, in summer 2006 the predawn pressure measurements documented an increase in available soil water between late June and late July (from −1 to −0.7 MPa). There was minimal rainfall in this 29-d period (<1 mm), while fog drip was recorded by our collectors on 16 of those days. Previous work has shown that addition of summer moisture pulses in semi-arid systems can lead to rapid increases in stomatal conductance and photosynthesis (Williams and Ehleringer 2000).

Sap flux data

Sap flux data averaged across all seven trees show clear correspondence with environmental conditions. Sap flux is sharply reduced under cloudy conditions, and it increases rapidly on days with large VPD, as has been shown by other investigators in foggy forest ecosystems (e.g., Burgess and Dawson 2004, Gotsch et al. 2014). Our sap flux data show fairly strong agreement with ETref at Site 9 (r^2 = 0.56, Fig. 4), particularly when using the sap flux data that have been partially corrected for ambient temperature gradients. Sap flux correlates well with

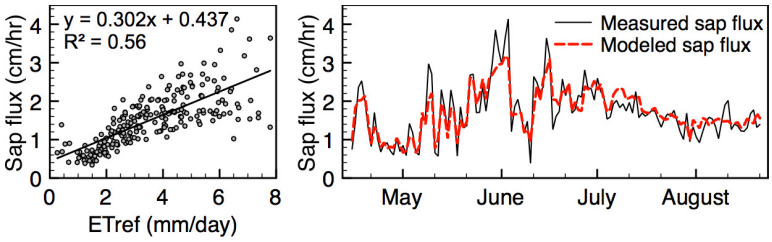

Fig. 4. Average sap flux velocity (cm/h) plotted against reference evapotranspiration (ETref, mm/d) at Site 9 on Santa Cruz Island (left panel). Average sap flux density in solid black and modeled sapflux density in dashed red for the period from mid-April to late August 2006 at Site 9 on Santa Cruz Island (right panel).

ETref except for anomalously high sap flux in late May and anomalously low sap flux in late July.

Despite the successes of the more mechanistically based ETref calculation, the statistical model created with random forest has higher predictive capability and low bias and error (r^2 = 0.8, MBE = 0.004, RMSE = 0.917, and MAE = 0.692; Fig. 4). Importantly, the random forest algorithm identified a running sum of summertime fog drip measured by our collectors to be one of the three most important predictor variables (including mean daytime VPD and PAR), of many that were tested. Day-to-day variations in sap flux are dominated by variations in PAR and VPD, as has been shown in numerous previous studies. Therefore, it is challenging to disentangle the effects of fog drip, which is also associated with large changes in PAR and VPD (Fischer et al. 2009), on daily sap flux variations. But we believe the running fog sum predictor implicitly captures the role that fog drip plays in maintaining sufficient soil water to sustain sap flux well into the summer after the last rainfall of the prior wet season (which fell during the night of 21–22 May 2006).

The seasonal time course in sap flux, from January to August 2006, is in general agreement with the seasonal trajectory of tree growth (next section). However, the peak in sap flux in 2006 (June) occurs roughly 1 month later than the peak in tree growth for that year. This is a time of year when the soils are still wet from the previous winter's rains, while also receiving regular inputs of summertime fog drip (Fig. 2). Notably, sap flux in summer 2006 was about the same magnitude as in the previous winter and spring, and stayed high until approximately the middle of July before declining. The timing of this decline in sap flux agrees well with the reduction in soil water potential in the upper surface layers during this same time period in the previous summer (8 and 15 cm depths under the tree canopy; Fig. 2a), and broadly agrees with the decline in soil water potential measured at deeper levels in late summer 2006 (Fig. 2c). As discussed above, surface soil water potential is strongly affected by summertime fog drip, and thus presumably plays a large role in maintaining summertime sap flux values at fairly high levels as is suggested by our statistical model results.

Tree growth data

Dendrometer data show near year-round growth in this moderate climate, with the exception of September 2004, when few trees were banded. Peak tree growth was concentrated in late spring and early summer of 2005 and 2006 (Fig. 5). Peak growth corresponds to warm weather shortly after the end of the rainy season. As with the seasonal time course of sap flux, stem growth throughout the rain-free and otherwise dry summers of 2005 and 2006 requires continued uptake of soil moisture, which raises the question of how and where soil moisture is acquired by the trees, particularly in 2006 when winter rainfall was normal and no late rains fell. Specifically, were trees relying to a measurable extent on summertime fog drip, or was the fog drip merely enhancing upper soil moisture layers and possibly stem water potentials?

Rain, fog, and stream water isotopic analyses

Assessing the proportional contributions of fog and rain inputs to soil water and plant water using isotopic analysis can help address whether trees take up and use summer fogwater,

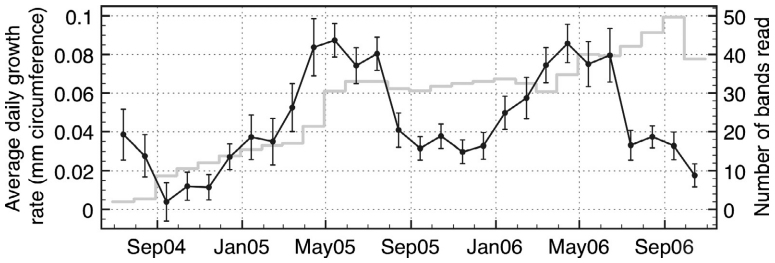

Fig. 5. Monthly mean change in circumference for Bishop pines (*Pinus muricata* D. Don) on Santa Cruz Island with standard error bars. Number of bands read (gray line) is reported as a rate of bands per month, taking into account the number of days between successive readings of each band. Data were smoothed for plotting by binning daily data into months (Williams 2006).

as the isotopic composition of dry season fogwater is quite stable and is consistently enriched relative to winter rainwater, as expected due to differences in source region and residence time in the atmosphere (Gat 1996, Dawson 1998). Volume-weighted seasonal averages and standard deviations for fogwater and rainwater from 2004 to 2006 are reported in Table 1. The isotopic offset between fog and rain is on the order of 2–3‰ for $\delta^{18}O$ and 15–20‰ for $\delta^{2}H$, with fairly high standard deviations for winter rainfall in particular. These isotopic offsets are comparable to a number of other coastal and montane ecosystems where fog and rain have been measured isotopically, but they are notably smaller than the isotopic offsets measured in northern California (Scholl et al. 2011).

Within any given month, rainwater isotopic composition is fairly homogenous across the transect (Fig. 6). Eight of 13 months analyzed show essentially no spatial isotope gradient. The five remaining months, however, show at least some differences across the transect, with the most prominent spatial variation being the late rainfall sample from May 2005. There is no systematic isotopic enrichment of rainwater from coast to inland, as would be expected if evaporative enrichment from the sample bottles were a significant problem prior to adding mineral oil and insulation (given the higher surface solar

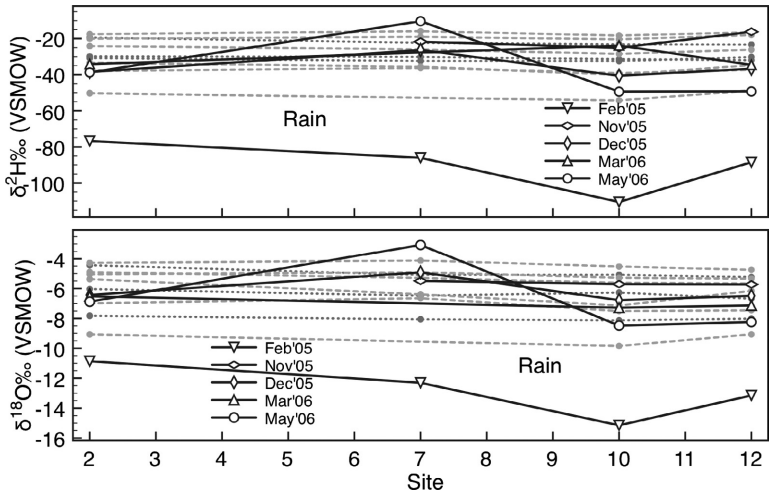

Fig. 6. Isotopic composition of rainwater across the Santa Cruz Island Transect. Months without spatial differences in isotopic composition are plotted in gray. Winter 2004–2005 samples are shown dashed, while winter 2005–2006 samples are darker dotted lines. Site numbers correspond to increasing distance from the coast along transect (Fig. 1).

energy and potential evaporation at inland sites). The differences in the February 2005 sample (Fig. 6) are attributed to differing quantities of rain from two storms that occurred 2 weeks apart and were isotopically distinct. One that originated in central Alaska yielded extremely depleted rainwater (δ^2H less than −120‰), while the other entrained large amounts of relatively enriched subtropical moisture (Fischer and Still 2007). Most of the differences in other months can be explained similarly.

For the 2005 dry season, we analyzed isotopic values of fogwater across the SCI transect (Fig. 7). There was minimal seasonal variation in fogwater isotopic composition (in both δ^{18}O and δ^2H), with the most variation occurring between early and late June of 2005. Fogwater isotopic composition was also fairly consistent across sites during each month, with a slight depletion from coast to inland. This trend also suggests that evaporative enrichment in our fogwater collection bottles was not a significant problem in the fog bottles.

The isotopic composition of the stream water was quite consistent across the time period analyzed (December 2003–January 2005; Table 1). We interpret the consistency as indicative of a large aquifer that integrates the rainfall signal over multiple years. There is a slight trend toward depletion in both isotopes over the dry season (not shown) that may be indicative of stratification within the aquifer, as the depletion is not consistent with either evaporation from the aquifer or fogwater additions during the dry season.

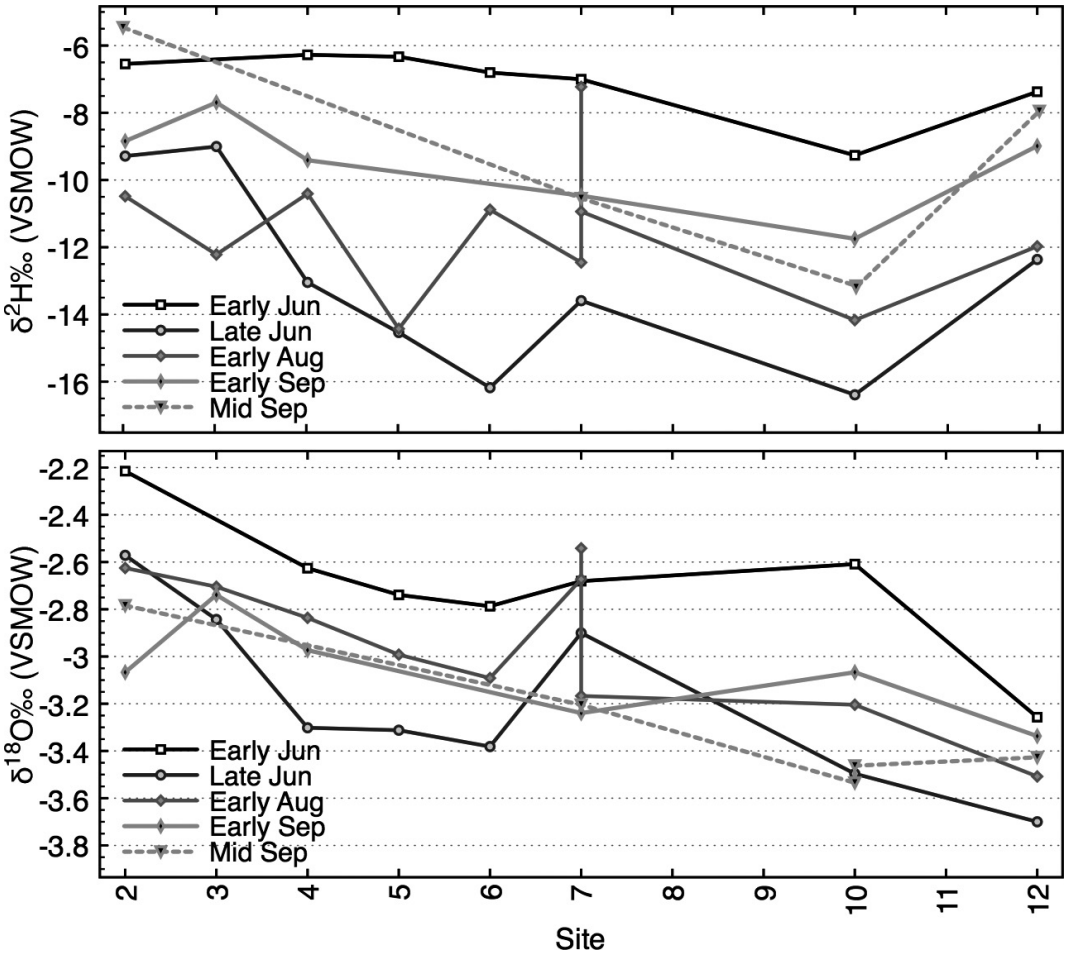

Fig. 7. Isotopic composition of fogwater across the Santa Cruz Island Transect during the 2005 dry season. Sites are numbered from the coast inland as in Fig. 1.

Soil and xylem water isotopic analyses

Soil water isotopic composition is derived both from rain and fogwater and subsequent evaporative fractionation effects. In general, surface soils are substantially enriched in both δ^2H and $\delta^{18}O$ during all sampling events compared to deeper soils, a phenomenon observed in other arid and semi-arid systems (Allison et al. 1983, 1987, Yakir and Wang 1996). This strong surface enrichment has also been observed in laboratory experiments (Miller et al. 1999) and simulations (Riley 2005). Water samples extracted from our soil samples generally plot on δ^2H-$\delta^{18}O$ lines with slopes considerably below the Local Meteoric Water Line (LMWL) for October–May rainwater samples (LMWL: $\delta^2H = 7.1 \times \delta^{18}O + 12.1$). This LMWL is fairly close to the relationship established for California (Kendall and Coplen 2001, Corbin et al. 2005). Similarly, the deuterium excess (dxs = $\delta^2H - 8 \times \delta^{18}O$) values for our soil samples are generally lower than the value expected for the LMWL (i.e., <12.1‰). While fog drip would also cause isotopic enrichment compared to rain percolating into the upper soil profile, it is difficult to disentangle the two effects (but see Corbin et al. 2005). However, the lower slope and dxs values of our soil samples are best explained by at least some soil evaporation causing isotopic enrichment through kinetic fractionation (Allison et al. 1983, Berkelhammer et al. 2013).

Isotopic values of water extracted from surface soils (0–3 cm) in 2005 show a sharp depletion following three rainstorms between 28 April to 9 May 2005 (not shown). Gradual enrichment follows, which is consistent with both evaporative enrichment and addition of relatively enriched fogwater with average $\delta^{18}O$ values of −2.8‰. Soil water profiles from core samples at Site 7 collected on consecutive summer days (20–21 June 2006) with overnight fog drip were analyzed for their isotopic composition. The results show distinct water strata and also temporal changes before and after the fog event. Notably, at all depths the soil water samples collected after the overnight fog drip event are slightly enriched compared to the day before, except for δ^2H at the shallowest depth (Fig. 8). On 20 June, soil water between 10 and 18 cm depth is more depleted in both isotopes than volume-weighted average winter rain. There is a stratum of relatively enriched water at 21 cm, and then more depleted water deeper in the soil profile. The soil profile taken on 22 June at Site 9 (1.9 km ENE) shows a similarly steep soil moisture profile in

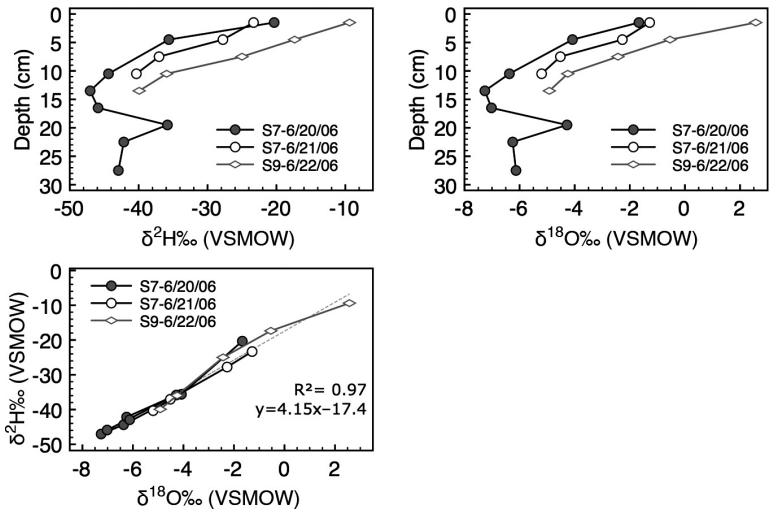

Fig. 8. The top panels show isotopic composition of vertical soil water profiles at two sites across 3 d in late June 2006. Soil cores were taken at Site 7 on the evening of 20 June 2006 and again the following morning after significant overnight fog drip. Soil cores were also taken at Site 9 on 22 June 2006. The bottom panel shows δ^2H-$\delta^{18}O$ plot of all extracted soil water samples with a slope that is consistent with kinetic isotope fractionation during evaporation.

the surface soil, with even greater enrichment in the uppermost layers. This additional enrichment is most likely due to reduced canopy cover at Site 9, and thus greater soil evaporation. Modeled ETref values at Site 9 are ~16% higher than at Site 7 in 2006; additionally, this Site is consistently brighter, hotter, and drier than Site 7, and the differences are due principally to lower cloud shading at Site 9 (Carbone et al. 2012). Water samples extracted from all soil profiles in late June 2006 (two dates at Site 7 and one date at Site 9) plot on similar δ^2H-$\delta^{18}O$ lines with slope and dxs values considerably below the LWML (Fig. 8, bottom panel).

Xylem water isotopes

Pine xylem water isotopic composition collected across the SCI transect throughout the study duration (Fall 2004 to Spring 2006) is shown in Fig. 9. Winter 2004–2005 xylem water isotopic values converge toward the seasonal volume-weighted average rain value of δ^2H −37.0‰ (Fig. 9a, Table 1). Subsequent xylem water isotopic enrichment through the summer is consistent with shallow root uptake of fog drip. Figure 9b also displays xylem water isotopic composition across the SCI transect for the 2005 dry season only. Between 5 June and 28 June 2005 all sites show a sharp depletion in δ^2H. We interpret the higher values in early June as a result of the trees drawing water from shallow soils that were wet in early June (Fig. 2a) with the relatively enriched rainwater from 28 April and 9 May (δ^2H −19.0‰; Fig. 6) and more enriched fogwater (seasonal average δ^2H −8.0‰; Fig. 7). The depleted xylem water isotope values later in the month suggest that shallow soils were drying out, and thus more water was drawn from deeper soil layers with water that more closely matched the mean isotopic composition of winter rainfall. Individual pine xylem water shows significant variability over space and time, and this variability illustrates local-scale effects that must be considered in stable isotope analyses. For example, the pine at Site 4, on a convex slope surrounded with bare soil, and subject to relatively high fogwater inputs, shows the most consistently enriched

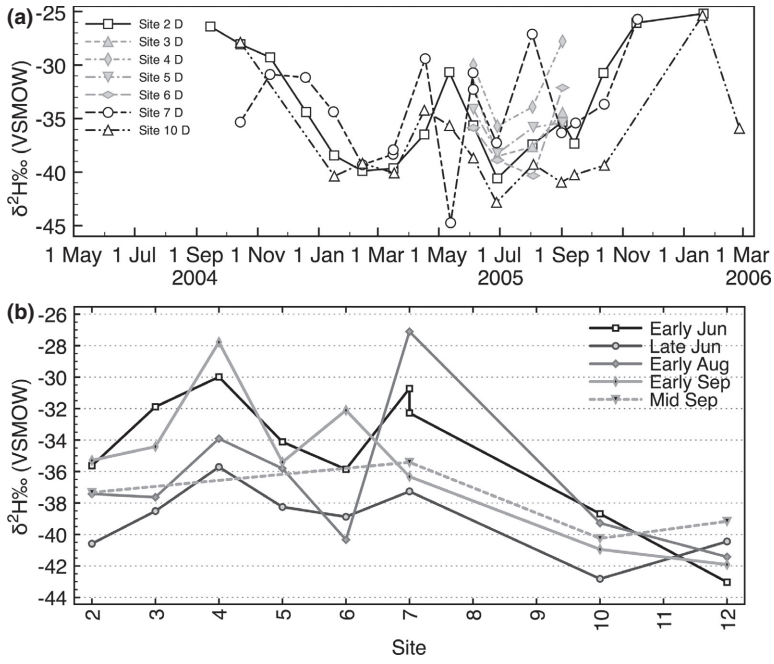

Fig. 9. (a) Isotopic composition of xylem water samples over time. Samples were analyzed from seven sites on Santa Cruz Island. Samples from Sites 3 to 6 (in gray) were only analyzed for the 2005 dry season. (b) Isotopic composition of xylem water samples across the SCI transect in summer 2005. Sites are numbered from the most coastal site to the most inland site.

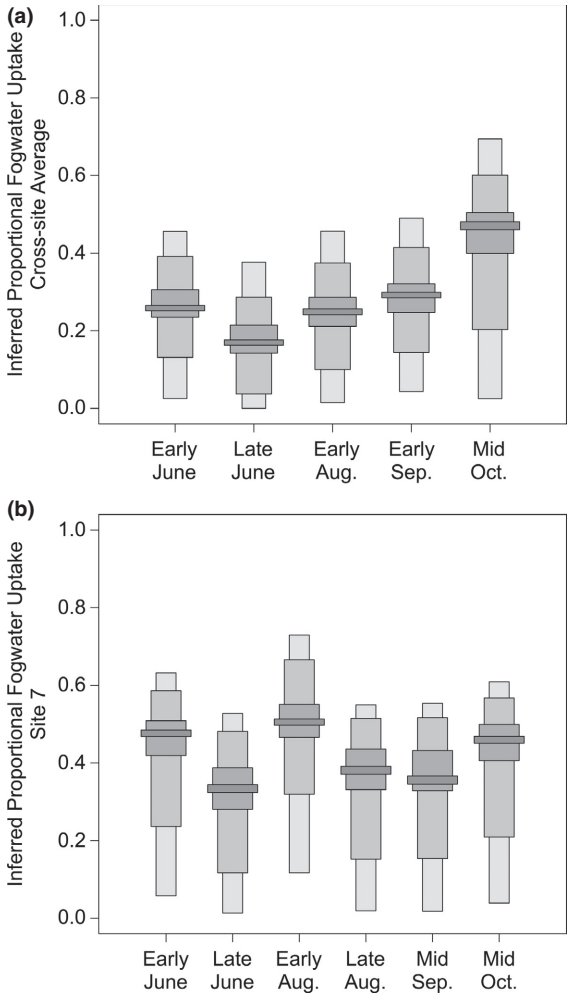

Fig. 10. (a) Inferred proportional fogwater contributions to xylem water during each sampling event (averaged across sites) during the 2005 dry season using volume-weighted mean isotopic values for fog and rainwater sources from the 2004 to 2005 winter and 2005 summer. Boxplots display the 5%, 25%, 75%, and 95% credibility intervals. (b) Same as (a) but for Site 7 during the 2005 dry season using volume-weighted mean isotopic values for fog and rainwater sources from the 2004 to 2005 winter and 2005 summer.

xylem water. The pine at Site 7 also has relatively enriched xylem water, in particular a large enrichment in early August. This sample was taken the day after a heavy overnight fog event.

The Bayesian isotope mixing model (SIAR) results bolster this descriptive analysis of xylem water isotope dynamics. In particular, the model outputs provide support for a small amount of fogwater uptake when analyzed spatially (at a single time point across sites) or temporally (at a single site through time). After averaging pine xylem water isotope values across transect sites during each dry season (May–October) sampling event in 2005, fogwater proportions calculated by SIAR are shown in Fig. 10a. Model outputs include a range of possible fogwater proportions in the xylem water. Importantly, the distributions of inferred possible source water contributions (i.e., the probability density functions) for fog and rain do not overlap in four of the five sampling periods; fog and rain proportions overlap only in the mid-October sampling, when samples were collected at only three sites on the transect.

Averaged across sites, the model infers at least some fogwater uptake in every sampling period (i.e., the probability of zero proportional fogwater uptake is very low). However, the inferred fogwater proportions have fairly wide ranges for a given sampling event; in early September, for example, the inferred fogwater proportions range from ~0.05 to ~0.5. Focusing on just the modes (i.e., the highest probabilities) of these inferred proportional contribution distributions, the SIAR outputs suggest fogwater proportions ranging from 0.17 to 0.28 for the four best resolved sampling periods (excluding the mid-October sampling). The SIAR outputs also support our earlier inference of variations in rooting depth contributions, like the change in shallow to deep soil moisture usage from early to late June. When focusing on a single site across the summer 2005 dry season (Site 7), the seasonal variation in inferred fogwater uptake is larger, and the fogwater proportions (modes) and distributions are also larger as compared to the cross-site average analysis. The xylem water isotopic enrichment in early August after a heavy fog drip event at this site is especially notable (Fig. 10b). However, the spread in the probabilities is so large that fogwater contributions cannot really be distinguished from rain when only a single site is analyzed.

A simple sensitivity analysis shows how varying the source water input values changes the inferred fogwater contributions. The fogwater proportions in Fig. 10 were calculated using the average volume-weighted isotopic values for rain and fog samples collected across the study period (2004 through 2006) as water source end members. These multiyear averages should be

more representative for such calculations. By contrast, when using the volume-weighted average values for rain and fogwater from the previous winter (2004–2005) and contemporaneous summer (2005), the variability in the rain source water isotopic composition is expanded, particularly for δ^2H (Table 1). The much higher rainwater variability in this one winter (2004–2005) was driven largely by the highly varying winter 2005 storms discussed previously. When the 2005 xylem water isotope data are re-analyzed using the 2004–2005 average source water end-member values, the inferred fog proportion probability distribution is expanded. Additionally, the mode (highest probability) of fog proportion is raised (not shown).

It is important to note that the xylem water isotopic composition from these trees was also likely affected by upper soil water evaporation, in addition to enriched fog drip. Disentangling the impact of evaporative enrichment on soil water isotopes is challenging, but one approach was outlined in Corbin et al. (2005). A challenge in using this approach at other sites like ours is selecting values to use for an evaporative enrichment line to correct samples back to a LMWL. Making such a correction at our sites would reduce the inferred fogwater proportions even further. In summary, while the SIAR analyses seem to provide a fairly robust assessment of potential fogwater and rainwater contributions to xylem water, the complexities inherent in this system imply that even state-of-the-art mixing estimates can be misleading and offer a higher level of certainty than is really warranted.

Discussion

Soil water is the primary source of xylem water, and here we focus on how fog, rain, and evapotranspiration affect soil water (both water availability and isotopic composition), and on how changes in soil water affect xylem water. Predawn xylem pressure does not decline below about −1.0 MPa at Site 7 even in the late summer, despite surface soils being below −1.5 MPa. This suggests that the trees are accessing deeper soil moisture. This interpretation is supported by some xylem water isotope values being more negative than mean rain, but in agreement with deeper soil water isotope values. Water in the soil appears to be highly stratified by depth (Fig. 8). The isotopic composition of each stratum is a complex and time-varying mixture of isotopically variable winter rain, relatively consistent summer fog, and isotopically enriched soil water from upper soil layers. The mixture appears to be affected by downward transport following rain and fog drip events that moves pulses of enriched or depleted water through the soil profile. Xylem water isotopes suggest transitions between multiple strata of soil moisture over the course of the summer dry season. These transitions are consistent with soil moisture data showing vertically patchy soil water potentials, and episodic rewetting of surface soils following fog drip events.

The episodic nature of fog drip events (Fischer 2007), and time lags in tree water uptake Meinzer et al. (2006), suggest that monthly sampling, even if carefully timed, may miss a great deal of higher frequency variability in ecosystem water pools and fluxes. Even once-daily sampling may miss important variability in such a heterogeneous ecosystem. For example, Filella and Peñuelas (2003), working in a coastal Spanish shrubland, observed xylem water δ^2H changes of 2–25‰ between morning and afternoon on the same plants, which they interpreted as within-day changes in the depth of soil water being used by plants.

An additional factor complicating evaluation of ecological significance of fogwater for long-lived species is that there are seasonal and interannual changes both in availability of fogwater and also in the ecological responses to fogwater. From year to year, for instance, tree cores from Torrey pines on adjacent Santa Rosa Island only show increased growth in response to fog in medium to high rainfall years (Williams et al. 2008). The mechanism is hypothesized to be activity of shallow roots able to take up fogwater. Seasonally, decreased root activity during hot months has been shown to limit piñon pines' ability to take up water from light summer rainfall (Williams and Ehleringer 2000). Such seasonal and interannual changes in ecological responses complicate sampling and interpretation.

Another issue that would need to be resolved for quantification of fogwater uptake is the horizontal patchiness of soil water isotopes. Soil

water inputs are primarily from throughfall rather than from rain or fogwater directly. The isotope composition of throughfall can be modified substantially from above-canopy fog and rain by evaporative enrichment (Rhodes et al. 2006). Throughfall quantity can also vary significantly over very short distances as a function of canopy architecture. This issue poses particularly significant challenges on Santa Cruz Island, where pines grow in extremely heterogeneous open stands mixed with chaparral shrubs. These issues with spatial and temporal heterogeneity of fogwater availability necessitate careful melding of integrated measures of fogwater uptake across multiple spatial and temporal scales.

To characterize temporal variability in soil water isotope values, in addition to the expected depth stratification, methods development for consistently resampling the same location would be extremely helpful in this and similar locations. This would also allow integration over a larger area than what is sampled by soil cores, which are susceptible to biases from extreme spatial heterogeneity in isotopic composition. Gas wells installed in the soil might be useful for sampling the isotopic composition of water vapor in the soil (Fischer 2007). Previous research on quantifying fogwater uptake using natural-abundance stable isotope measurements has largely taken place in ecosystems with much lower evaporation. Additionally, this previous research has modeled soil water as consisting of basically two pools: shallow soil water isotopically matching summer fog, and deeper soil water matching the previous winter's rain (Ingraham and Matthews 1995, Dawson 1998, Ingraham and Mark 2000). Corbin et al. (2005) accounted for evaporation of surface soil water in a grassland study, but did not need to account for multiple strata of soil water with different isotopic values down through the soil profile due to the shallower rooting profile of grasses. Previous studies quantifying uptake of soil water from different depths using isotopes have dealt primarily with a consistent ground water source at the bottom of the rooting profile and limited variability in source waters above (e.g., Cramer et al. 1999, Cook and O'Grady 2006). In the xeric environment of Santa Cruz Island, the combination of isotopically diverse source waters, significant evaporative enrichment, depth stratification of both soil water isotopes and soil water potential, and above all the short-term temporal variability in all of the above factors, would require substantial new methods development to rigorously quantify fogwater uptake on physiologically relevant timescales.

Even without more rigorous quantification, however, summer fog drip does clearly raise soil water potentials and is taken up in detectable amounts by drought-sensitive Bishop pines during the long annual summer drought. Careful analyses of tree ring chronologies and climate records have also demonstrated the strong ecological importance of fog drip for coastal conifers in Southern California (Biondi et al. 1997, Williams 2006, Williams et al. 2008, Fischer et al. 2009). The ecological importance of fog has been shown to include influencing growth rates and stand boundary dynamics over time (Carbone et al. 2012). The strength of these effects, despite relatively minor amounts of fogwater uptake, suggests unusually strong ecosystem sensitivity to fog. Ecosystems sensitive to relatively small amounts of fogwater may require significantly greater sampling effort, sampling of varied ecological parameters across multiple scales, and/or methodological advances to quantify fogwater impacts.

Taken together, our data and analyses suggest a highly dynamic and spatially variable interaction between fog interception and water uptake by trees in this stand. This is likely to be the case in similar systems with highly variable and unpredictable water inputs. Water isotopes can play an important role in constraining the contributions of fog and rainwater, but they are also limited by geographical, physical, and biological factors specific to each system. A more extensive sensitivity analysis could be conducted to assess the potential for inferring fog and rain contributions with reasonable statistical accuracy given fog and rain end-members and associated uncertainty at other sites based on a meta analysis of fog and rain isotope data (Scholl et al. 2011). One challenge with using water isotopes to infer fog and rain contributions is that relatively seasonal ecosystems (e.g., Mediterranean climate zones) seem to have the largest isotopic separations between fog and rain. However, these ecosystems also experience the greatest influence of evaporative processes that complicate isotopic analyses. By contrast, while mesic ecosystems like Puerto

Rico and Hawaii should experience less evaporative enrichment, these systems also have much smaller isotopic separation between fog and rain (Scholl et al. 2011).

Even with our sampling limitations, it appears that this forest takes up significantly less summertime fogwater than some other California coastal forests like the coast Redwood (Dawson 1998). That said, fogwater clearly raises water potentials of soils, is taken up by plants during the long summer drought on Santa Cruz Island, reduces local VPD when it evaporates back to the atmosphere, and is ecologically important at the stand level (see Williams et al. 2008, Fischer et al. 2009, Carbone et al. 2012, Baguskas et al. 2016). The relatively high range of uncertainty in the proportion of fogwater usage demonstrates some limits of current methods, the challenges of working across scales, and the importance of carefully considering ecosystem sensitivity to fogwater uptake even in small amounts.

An improved understanding of ecosystem sensitivity to fogwater is critical for predicting how such ecosystems in this region will respond to climate change. The northern Channel Islands are right on the boundary of where the climate models project drying in southern California and wetting in central-northern California (Maloney et al. 2013, Seager et al. 2014), and thus the multimodel mean precipitation projection trends for the Channel Islands region are weak but also uncertain. The future of fog on the Channel Islands is also highly uncertain (Williams et al. 2015*a*). Wang et al. (2015) show that coastal upwelling should intensify but also migrate northward. Given that the upwelling-intensified temperature contrast between cold SSTs and warm air above the marine layer is a primary control of fog in this region (Schwartz et al. 2014, Williams et al. 2015*a*), we might expect increased fogginess off of the northern CA but with uncertain impacts in the Channel Islands region further to the south. Overall, global climate models are at odds regarding future trends in the subtropical stratocumulus regime (Webb et al. 2013, Bellomo et al. 2014, Qu et al. 2014). As for observed trends in our general study region, there are unfortunately no long-term (multidecade) cloud observations on Santa Cruz Island, but there are other Channel Islands that have records of hourly cloud-base height going back as far as the 1940s. In Williams et al. (2015*a*) it was shown that on two Channel Islands (San Clemente and San Nicolas), summer stratus frequency had slightly declined over the past 50–65 yr, but that fog frequency (frequency of very low stratus clouds) had somewhat increased. On the nearby Santa Barbara coast, there has been no detectable trend in fog frequency or overall stratus-cloud frequency.

While future trends in precipitation and fog are highly uncertain, it is much more certain that southern and central California will continue to get warmer in coming decades as a result of increased greenhouse forcing, enhancing evaporative demand and putting stress on many ecosystems reliant on near-surface soil moisture. This growing effect of anthropogenic warming is now detectable in calculations of the soil-moisture balance throughout mainland California (Williams et al. 2015*b*), highlighting coastal fog as a potential buffering mechanism that may provide refuge to ecosystems that can utilize fog drip during the warming and drying summer months.

Acknowledgments

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